Migration speed, routes, and mortality rates of anadromous brown trout S*almo trutta* during outward migration through a complex coastal habitat

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ABSTRACT: Little is known about migratory routes and habitat use of anadromous brown trout *Salmo trutta* at sea. We therefore conducted a 2 yr study (2011–2012) on sea trout in the River Himleån system (a river, an estuary, and a coastal sea environment) in western Sweden. The main objectives were to investigate migration speed, migration routes, and mortality both for adult brown trout returning to the sea (kelts) and smolts (generally 2 yr old trout migrating to the sea for the first time). Brown trout were captured and tagged with hydro-acoustic transmitters, after which they were released and monitored during their initial migration. Migration was primarily nocturnal in the river and estuary, whereas no tendency for nocturnal migration was observed along the coast. Migration speed tended to decrease as individuals progressed from the river through the estuary and along the coast, and we found no differences in absolute migration speed between kelts and smolts. Smolts and kelts showed similar mortality. Mortality during the initial part of the migration ranged between 5 and 51% and was significantly higher in 2011, for both smolts and kelts. Our study is the first to compare migratory patterns and mortality rates between sea trout kelts and smolts during the transition from freshwater into an open coastal system.

KEY WORDS: Sea trout · Telemetry · Kelt · Smolt · Swimming speed · Survival · Salmon

INTRODUCTION

Anadromous fishes play an important role in aquatic ecosystems (Eriksson & Muller 1982, Gresh et al. 2000, Näslund et al. 2015) as well as terrestrial ecosystems (Willson & Halupka 1995), e.g. as nutrient transporters and vectors for energy from the sea to lotic ecosystems. They also play an important economical role for fisheries, both recreational and commercial (Fiskeriverket 2010, Stensland & Baardsen 2012). For example, on the west coast of Sweden, brown trout *Salmo trutta* has become an important species for sport fishermen due to a rapid decline of other species such as Atlantic cod *Gadus morhua* in

the 1990s (Fiskeriverket 2010). Currently, anadromous brown trout abundance is at a stable level in the sea, but in many rivers, fish are threatened as a consequence of anthropogenic disturbances such as dams, weirs, and pollution (de Groot 2002, Östergren & Rivinoja 2008, Freyhof 2013).

The freshwater phase of anadromous brown trout has been well studied and reviewed in a number of books and articles (e.g. Elliott 1994, Klemetsen et al. 2003, Jonsson & Jonsson 2011). During this part of the life cycle (1–5 yr), trout are fairly stationary (Bohlin et al. 2002), with a generally high growth rate during the first year. As the trout increase in size, the growth rate slows down due to limitations in food

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abundance (Økland et al. 1993, Dodson et al. 2013). The trout can then either stay in the river and have a lower growth rate or migrate to the sea where the growth potential is higher (Northcote 1978, Gross et al. 1988, Cucherousset et al. 2005). Anadromous salmonids including brown trout undergo a transformation called smolting, in which the trout show several physiological and morphological changes preparing them for a life in the sea (Björnsson et al. 2011). Smolting is prompted by photoperiod and temperature, whereas the downstream migration is triggered by water discharge and temperature (Björnsson et al. 2011, Aldvén et al. 2015). Smolts generally start to migrate downstream during the spring and early summer, often in shoals, and sometimes in mixed shoals with fish from different species of a certain size group as seen in both Atlantic salmon *Salmo salar* and brown trout (Hvidsten et al. 1995, Stewart et al. 2006, Aldvén et al. 2015). The timing of migration is important for the early marine survival, as seen in Atlantic salmon (McCormick et al. 1998, Rikardsen & Dempson 2010), and the mortality rate during early marine migration can vary between 20 and 65% (Thorstad et al. 2007, Aarestrup et al. 2014, del Villar-Guerra et al. 2014), whereas the overall mortality in the sea has been reported to be as high as 95% (Berg & Jonsson 1990, Klemetsen et al. 2003, Jonsson & Jonsson 2009). The duration of the stay at sea varies between latitudes but also between individuals from the same natal river (Berg & Berg 1989, Klemetsen et al. 2003). However, the reason behind these individual differences remains unknown.

Little research has been done on sea trout migration within the marine environment. Previous studies on brown trout smolts have only investigated migrations through fjord systems (Moore & Potter 1994, Thorstad et al. 2004, 2007, Aarestrup et al. 2014, del Villar-Guerra et al. 2014). To our knowledge, no study has examined sea trout smolt migration through a complex open coastal habitat, and very few have investigated post-spawner (kelt) migration (Bendall et al. 2005).

In this study, we used acoustic telemetry to investigate the movement, rate of progression, and mortality of wild brown trout smolts and kelts as they migrate from the river out into an estuary and a coastal sea area (the Kattegat Sea, NE Atlantic). We predicted that the downstream migration of kelts would be faster than that of smolts, as has been observed in Atlantic salmon (Halttunen et al. 2009, Hedger et al. 2009). We also predicted that mortality rates would be higher in smolts compared to kelts during the initial phase of migration due to size-spe-

cific predation pressure (Jepsen et al. 1998, Aarestrup & Koed 2003, Skov et al. 2011). Earlier studies from the region have hypothesized that brown trout follow the prevailing currents along the coast once they reach the coastline (Svärdson & Fagerström 1982, Degerman et al. 2012), and thus we would expect them to migrate in a northerly direction on the west coast of Sweden.

To manage anadromous brown trout stocks, it is important to acquire information on home ranges and movement of brown trout in the sea in order to make regulatory decisions and implement conservation measures. To know where and when trout are in a certain area helps in the protection of threatened populations along the coastline. This study contributes as an indicator of how sea trout populations migrate along an open coastline, aiding in the management and conservation of this important resource.

MATERIALS AND METHODS

Study area

The study was conducted in the river and estuary of the River Himleån on the west coast of Sweden (57° 8′ 0.3″ N, 12° 15′ 3.7″ E), which stretches 38 km from the spring (76.7 m above sea level) to an inner estuary (Fig. 1). The inner estuary consists of a shallow (average depth = 40 cm) sand flat functioning as a bird sanctuary that was established in the 1930s and is inhabited today by a number of piscivorous bird species (e.g. Podicipedidae, Phalacrocoracidae, Ardeidae, Laridae, Sternidae, Pandionidae). In the middle part of the inner estuary are 2 deeper channels (<1.5 m), 1 northern and 1 southern. These 2 channels then merge into another shallow sand flat (<1 m) before reaching the outer part of the estuary which consists of stone reefs and small islands that create 4 pathways to the open sea. The depth in the outer estuary ranges from 1.5 to 8 m.

During the study period (March to September, 2011 and 2012) water discharges were calculated from observed water levels using a staff gauge attached to the smolt trap in the stream and flow measurements at different water levels. Water temperature (°C) at the smolt trap and in the estuary (at each receiver line) was measured every hour using a temperature logger (Onset, TidbiT v2 temperature logger). Turbidity was measured twice every day and divided into 2 categories: clear or turbid. The water clarity was determined by observing the staff gauge by the trap. The category 'clear' was given when the
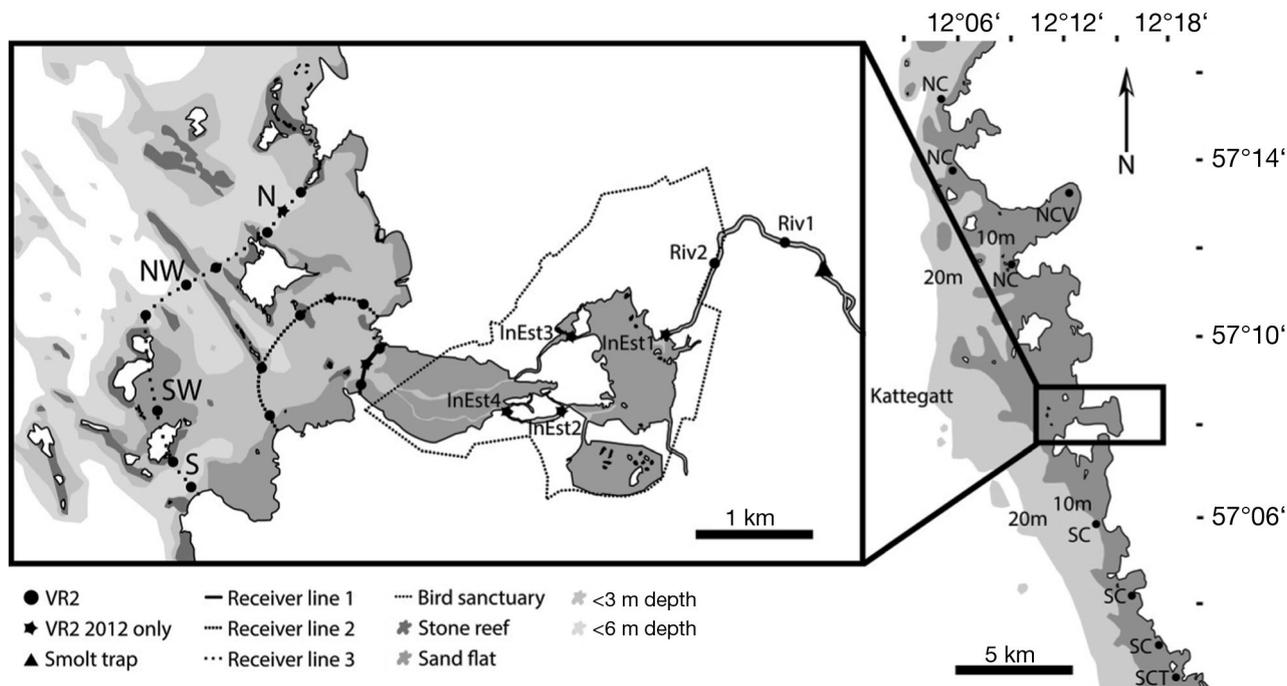
Fig. 1. River Himleån (west coast of Sweden), estuary, and coastline showing depth profiles and regions: River (Riv1 to Riv2), Inner estuary (Riv2 to Receiver line 1), Outer estuary (Receiver lines 1−3), Outer coast (Receiver line 3 to NC: north coast, SC: south coast, NCV: mouth of River Viskan, SCT: mouth of Tvååkers kanal). The receivers in the Inner estuary were not present in 2011. Sand flat depth varies from 0.3 to 1 m and stone reefs from 0 to 1.5 m. Exit channels from the outer estuary are shown as: north exit (N), northwest exit (NW), southwest exit (SW), and south exit (S)

lowest white 10 cm section (the section nearest the bottom) was visible, and the category 'turbid' was given when it was not visible. Water level (m) was measured on an hourly basis in the transition zone between the inner and outer estuary using a depth data logger (Onset, HOBO U20-001-04-Ti Data Logger). Salinity (practical salinity units, PSU) in the outer estuary (at the second receiver line) was measured every hour at 1 m depth using a conductivity data logger (Onset, HOBO U24-002-C.

Tagging and capture of sea trout

Brown trout were captured using a smolt trap, which was operated from 17 March to 20 May 2011 and from 16 March to 12 June 2012. The trap consisted of an aluminum box (length × width × height: 174 × 152 × 110 cm) covered in steel mesh (0.9 cm mesh size) placed approximately in the middle of the stream 2 km upstream of the estuary (Fig. 1). Two steel racks were spread from the trap to each side of the river in order to lead the smolt into the trap box. The trap was emptied twice a day throughout the migration period (for details see Aldvén et al. 2015).

In 2011, 80 smolts (fork length 180 ± 15.2 mm SD) and 20 kelts (fork length 382 ± 85.1 mm) were equipped with individually coded acoustic transmitters (Thelma AS LP 7.3, diameter: 7.3 mm, length: 18 mm, weight in air: 1.9 g; and LP 13, diameter: 13 mm, length 26 mm, weight in air 7.3 g, respectively, pulse interval 20/60 s), and in the following spring (2012), 99 smolts (167 ± 16.1 mm) and 20 kelts (464 ± 95 mm) were equipped with Vemco V7 transmitters (V7-4x-069k-3, diameter: 7 mm, length: 18 mm, weight in air: 1.4−1.8 g, pulse interval 20/60 s). The switch in transmitter model was due to a problem with short battery life in the Thelma tags. Before surgery, fish were individually anesthetized by submergence in a bath containing 2-phenoxy-ethanol (0.7 ml l^{-1}, average 3 min). An incision to the ventral surface in front of the pelvic girdle was made, through which the transmitter was inserted and gently pushed into the body cavity. The incision was then closed with 2 independent sutures using a poly-filament suture (Ethicon Prolene 5-0). The smolts were tagged in several batches (9 in 2011, 4 in 2012) from 19 April to 10 May 2011, and from 18 April to 10 May 2012. Fish fork length (mm) was measured for all tagged fish, and the sex of kelts was determined using visual cues, including

head size in relation to the body size (Niemelä et al. 2000), but mainly jaw morphology; the fish was classified as male if a kype was present. The fish were then left to recover in a tank for 8 h before being released back into the river. Tagged smolts were released along with untagged smolts into a flow-through container within the river, from which they could leave at any time; kelts were released directly back into the river. The container within the river was checked every night after tagging, and only a small number (1 to 5 individuals) of smolts remained in the tank at this time; often these individuals were from the untagged group.

Tracking

Fish tracking was performed using 24 (2011) and 31 (2012) automatic acoustic listening stations (Vemco VR2 and VR2W) deployed in a fixed array (Fig. 1). The study system was divided up into 4 different sections: (1) river (Riv1 and Riv2), (2) inner estuary (Riv2 to Receiver line 1), (3) outer estuary (Receiver line 1 to line 3), and (4) outer coast (Receiver line 3 to north and south coast). Stations along the coastline covered a distance of 30 km from north to south, and included the mouths of 2 neighbouring rivers (River Viskan and Tvååkers kanal). Listening stations in the river and estuary were placed to maintain coverage (overlap of detection range between the listening stations), and several range tests throughout the study period revealed a near-constant detection range over the time of the study. The receivers along the north and south coast were used to give information on the direction of migration once the fish left the system. The receiver range in the outer estuary was estimated by towing an acoustic transmitter (Thelma AS LP 7.3) behind a kayak across the outer estuary in 2011. Detection range varied at the different receiver locations: 50 to 200 m within the river, 25 to 30 m within the estuary, 100 to 150 m along Receiver line 1, 500 to 600 m along Receiver lines 2 and 3, and 400 to 600 m at the coastal receivers. Range tests revealed that the Vemco tags had a shorter transmission range (20 to 40 m shorter) than Thelma tags, so extra listening stations were deployed in the inner estuary region to maintain detection coverage in 2012 and to better resolve migration through this part of the system. One of these receivers was placed at the mouth of the river, enabling determination of the time spent in the river. Data collection was made weekly from deployment in March to the end of the study in September in both years. False detections were removed

using the method outlined by Vemco (2012): the First Scan Acceptance Criteria resulted in removing 0.01% of detections. Manual tracking was performed using a VR100 and a directional hydrophone (Vemco, VR100 Acoustic Receiver, Hydrophone type: VH110 [50–85 kHz]) in the river and estuary (outside the bird sanctuary) during both years, 1 mo after the last batch of fish was tagged, in order to assess predation and to locate individuals that were lost between receivers. Individuals within the river were positioned to <2 m and those that were detected in shallow areas were disturbed (by shifting stones and sediments) in order to assess whether they were alive or dead.

Statistical analysis

Influences of environmental and morphological factors on residence time (the time of stay within an area) were analyzed using generalized linear modeling. Residuals were modeled using a Gamma distribution (using R function glm [stats], link = log), and backwards selection was used to simplify models, with the model with the lowest Akaike's information criterion (AIC) being selected. Models were fitted to determine:

(1) the effect of sex, body length, and year on residence time for kelts across the entire river-estuary system (see Eq. 1 below);

(2) the effect of body length, life stage, and year on residence time across the entire river-estuary system (Eq. 2 below);

(3) the effect of body length, life stage, river discharge, and river temperature on residence time within the river for 2012 (residence time within the river could only be determined for 2012 because of the receiver configuration) (Eq. 3 below);

(4) the effect of sex, body length, river discharge, and river temperature on residence time within the river for kelts in 2012 (Eq. 4 below).

$$Y = \beta_0 + \beta_1 Sex + \beta_2 BodyLength + \beta_3 Year + \varepsilon \quad (1)$$

$$Y = \beta_0 + \beta_1 BodyLength + \beta_2 LifeStage + \beta_3 Year + \varepsilon \quad (2)$$

$$Y = \beta_0 + \beta_1 BodyLength + \beta_2 LifeStage + \beta_3 Discharge + \beta_4 Temperature + \varepsilon \quad (3)$$

$$Y = \beta_0 + \beta_1 Sex + \beta_2 BodyLength + \beta_3 Discharge + \beta_4 Temperature + \varepsilon \quad (4)$$

where β_0 is the intercept, sex has 2 levels (male and female), stage has 2 levels (kelt and smolt), and ε is the error of the model. Residence time across the full river-estuary system was determined from the first detection in the river to the first detection at Receiver

line 3 in the outer estuary. Residence time within the river was determined between first detection in the river and first detection at the mouth of the river (2012 data only). The effect of temperature and salinity on the residency time in the inner estuary as well as entry into the inner estuary was analyzed using a Pearson's χ^2-test.

Ground speeds (body lengths [BL] s^{-1} and m s^{-1}) were calculated for 2012 between successive receivers: (1) in the river, using the time between first detection at InEst1 (see Fig. 1) from previous detection at Riv1 over the measured distance along the river; (2) inner estuary, first detection at Receiver line 1 from the first previous detection at InEst1, over the measured distance through the inner estuary; (3) outer estuary, first detection at Receiver line 3 from the first previous detection at Receiver line 1, over the calculated Euclidean distance between the detecting receivers; and (4) outer coast, using the mean time between successive detections between receivers along the coast and the measured distance between receivers. Ground speeds along the coast are not comparable to the other parts of the system due to the open nature of the system. Differences in ground speeds between regions were tested with a Kruskal-Wallis test.

Estimated mortality within the river and inner estuary was quantified as the percentage of fish that did not have a final detection in the outer estuary or coast. This was based on the assumption that all sea trout leaving the river and inner estuary would have been detected by a receiver outside of these regions (in the outer estuary or along the coast) on their seaward migration. Instantaneous mortality rates (z) from release until final detection within the entire receiver array were modeled using a parametric survival model (R function *survreg* in the *survival* package of R). Life stage and year were additive predictors in the model. The daily mortality rate (M), expressed as a percentage per day, was calculated as $M = 100 \times (1 - e^{-z})$.

RESULTS

Environmental measurements

The mean ±SD River Himleån discharge was 2.42 ± 1.21 m^3 s^{-1} (range 0.99–5.33 m^3 s^{-1}) in 2011 and 2.03 ± 0.96 m^3 s^{-1} (range 1.07–5.67 m^3 s^{-1}) in 2012, and the ratios between clear and turbid water were 51:14 and 69:20 in 2011 and 2012, respectively. Water temperature in the river ranged from 2–4°C in the beginning

of the study period to 13–17°C at the end for both years. Water temperature in the estuary ranged from 6–8 to 16–22°C during the same period. Mean water level during the study was 1.05 ± 0.13 m (range 0.48–1.5 m), and the tidal range was found to be very low, with a range of 10 cm from daily lowest to highest reading in both years. Salinity at Receiver line 2 in the estuary ranged from 9.1 to 16.1 PSU during the study period.

Telemetry efficiency

The validation study made by towing a transmitter through the outer estuary showed that 23.3% of the area of the outer estuary was left uncovered by the receiver array, typically in a swath between Receiver lines 2 and 3. However, all exits of the estuary were covered by the maximum range of the receivers, so it was unlikely that fish could exit the estuary without being detected. Only 1 individual detected at a receiver on the coast in 2011 (out of 24 detected) had passed the receivers in the outer estuary without being detected, and no individuals in 2012 passed the receivers in the outer estuary without being detected. River detection in 2012 was poorer. In the outer estuary in 2012, 11 individuals (out of 92 detected) were not detected previously in the river. This contrasts with 2011, where all individuals detected in the outer estuary were previously detected in the river. The fact that individuals could pass through regions without being detected will have slightly biased our estimates of mortality, but this effect was small. For example, the 1 individual that was not detected in the estuary out of the 24 that were detected on the coast in 2011 would have negatively biased estimates of mortality by ~4% in the river-estuary system.

Overview of migration through the system

A large range of migration patterns of individuals through the system was found, with smolts showing a larger variation in residence time than kelts in the river and estuary (Fig. 2). In both years, and for both smolts and kelts, most individuals (66.7% in 2011; 100% in 2012) left the river by mid-May (Fig. 2). A greater percentage of individuals released in 2012 were detected at receivers along the coast (42% of smolts and 55% of kelts) than for individuals released in 2011 (24% of smolts and 25% of kelts), suggesting higher mortality in 2011. Body length and sex had no
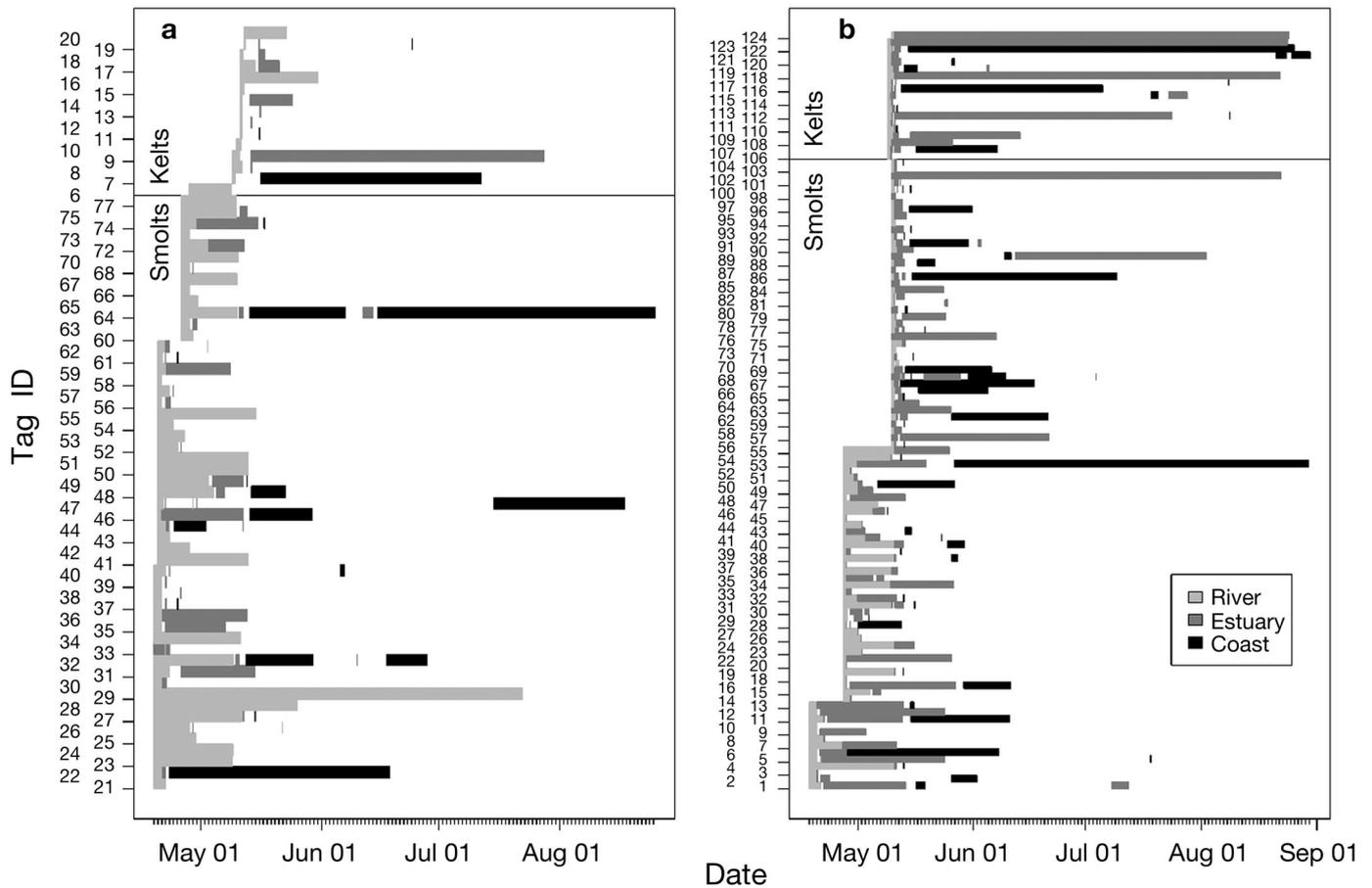
Fig. 2. Region of residence of anadromous brown trout *Salmo trutta* by date in (a) 2011 and (b) 2012. Inner and outer estuary are grouped

effect on residence time across the entire river and estuary system; residence time was significantly shorter in 2012 (Table 1). We also observed a nocturnal migration pattern in the river, estuary, and inner coast which was not present in the outer coast (Fig. 3).

Table 1. Generalized linear model showing relationship between residence time within the river, inner and outer estuary, and sex, body length, and year for kelts of anadromous brown trout *Salmo trutta*

	Estimate	SE	t	$Pr(>|t|)$
Initial model				
(Intercept)	0.936	0.867	1.079	0.291
Body length	0	0.002	0.175	0.863
Sex: Male	−0.092	0.295	−0.313	0.757
Year: 2012	−0.781	0.312	−2.506	0.019
Final model				
(Intercept)	1.046	0.215	4.873	<0.001
Factor(Year)2012	−0.778	0.275	−2.824	0.009

River

Migration through the river could be analyzed for 91 individuals (72 smolts and 19 kelts) out of the 119 released, which had detections both in the uppermost receiver in the river and in the mouth of the river in 2012.

Downstream migration started in early April, and the tagged individuals migrated downstream from late April to mid-May, a period where a large variety of migration strategies was observed (Fig. 2). Migration within the river was significantly faster compared to both the inner and outer estuary (Kruskal-Wallis test: $\chi^2 = 12.01$, p = 0.002 for smolts and $\chi^2 = 24.65$, p < 0.001 for kelts). In 2012 (where the exact time of departure from the river could be determined from the receiver at the river mouth, InEst 1; Fig. 1), residence time within the river was negatively related to discharge (Table 2). Mean ± SD ground speeds within the river were 0.17 ± 0.14 and 0.10 ± 0.03 BL s^{-1} for smolts and kelts, respectively, al

though smolts, being smaller, migrated slower in absolute terms (0.29 ± 0.25 m s^{-1} for smolts and 0.44 ± 0.15 m s^{-1} for kelts). Smolts showed a greater varia-
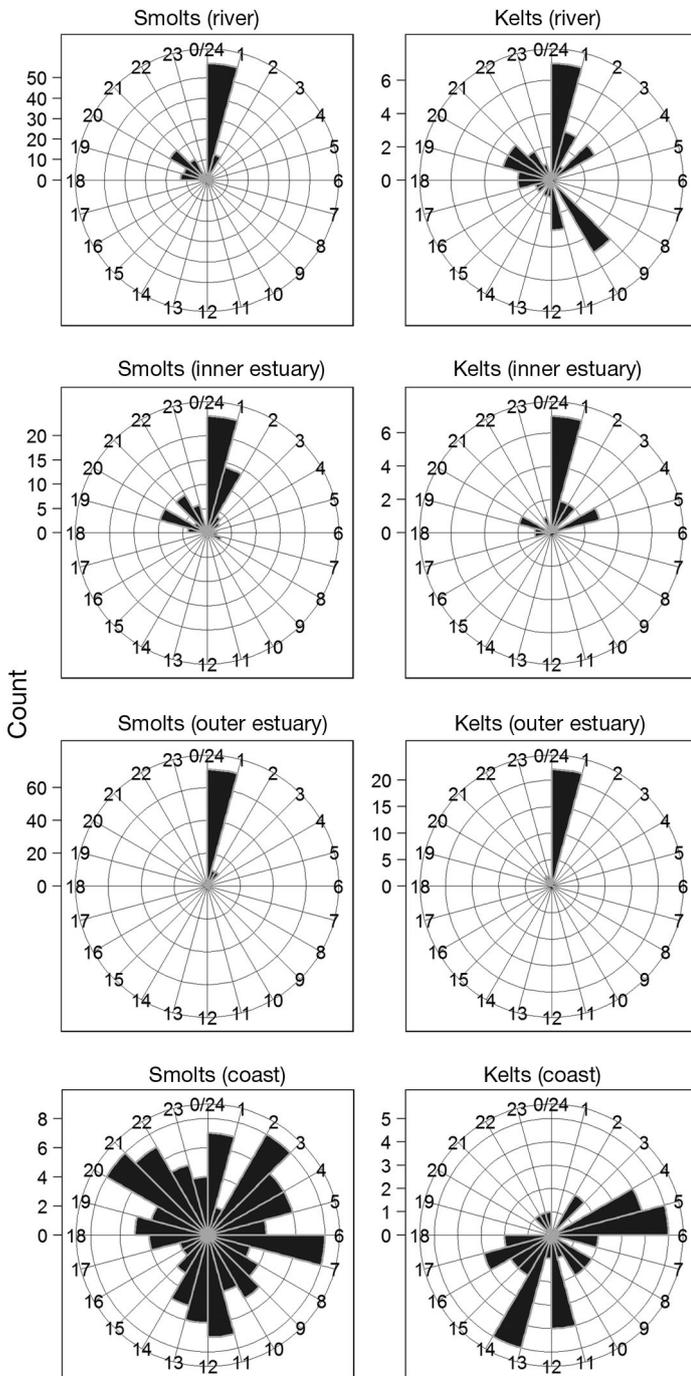

Fig. 3. Hourly distribution of first detections for smolts and kelts of anadromous brown trout *Salmo trutta* in the river, inner estuary, outer estuary, and coast. For the coast, first detections were defined as occurring when an individual moved to a coastal receiver from another receiver (either coastal or from the outer estuary). Data are pooled from 2011 and 2012

Table 2. Generalized linear model showing relationship between residence time within the river and body length, life stage, river discharge, and temperature in 2012 for anadromous brown trout *Salmo trutta*

	Estimate	SE	t	Pr(>|t|)
Full model				
(Intercept)	−0.21	2.679	−0.078	0.938
Discharge	−0.491	0.119	−4.105	<0.001
Temperature	−0.158	0.199	−0.794	0.429
Stage: smolt	2.685	1.392	1.929	0.057
Body length	0.002	0.004	0.510	0.611
Final model				
(Intercept)	−0.641	0.496	−1.292	0.2
Discharge	−0.545	0.093	−5.862	<0.001
Stage: smolt	2.058	0.44	4.672	<0.001

Table 3. Generalized linear model showing relationship between residence time within the river and sex, body length, river discharge, and temperature in 2012 for kelts of anadromous brown trout *Salmo trutta*

	Estimate	SE	t	Pr(>|t|)
Full model				
(Intercept)	13.379	12.001	1.115	0.284
Discharge	−0.048	0.229	−0.211	0.836
Temperature	−0.502	1.191	−0.421	0.68
Length	0.003	0.002	1.335	0.203
Sex: Male	−0.731	0.351	−2.083	0.056
Final model				
(Intercept)	7.883	0.918	8.591	<0.001
Length	0.003	0.002	1.394	0.182
Sex: Male	−0.75	0.336	−2.236	0.04

tion in residence (mean $\pm$ SD = 0.99 ± 2.09 d) time within the river compared to kelts (0.79 ± 0.08 d). Further, for kelts, males migrated significantly faster than females from the position of release to the receiver at the river mouth in 2012 (Table 3).

Inner estuary

Most individuals (96 of 99 individuals, 97%) tended to move quickly through the estuary, although some individuals remained within the estuary for a longer period of time (2011, median = 2.51 d, min = 0.44 d, max 78.07 d; 2012, median = 2.55 d, min = 0.14 d, max 106.2 d). In 2012, individuals used the northern (n = 40) and southern channel (n = 34) in the inner estuary. Ground speed within the estuary was significantly slower than within the river (Kruskal-Wallis test: χ^2 = 8.46, p = 0.004 for smolts and χ^2 = 17.05, p < 0.001
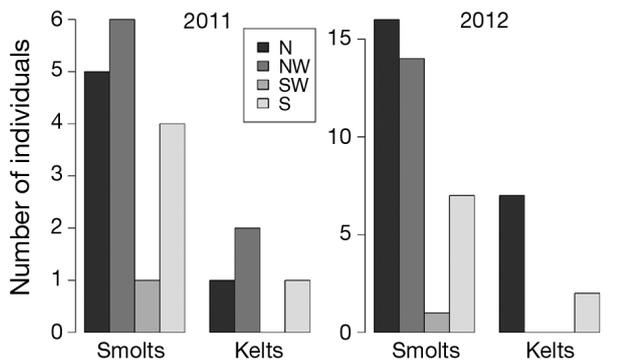
Fig. 4. Channel of first exit for individual anadromous brown trout *Salmo trutta* detected in Receiver line 3 according to life stage: north exit (N), northwest exit (NW), southwest exit (SW) or south exit (S) (see Fig. 1)

for kelts), with an average speed of 0.06 ± 0.05 BL s^{-1} (0.10 ± 0.09 m s^{-1}) for smolts and 0.01 ± 001 BL s^{-1} (0.06 ± 0.05 m s^{-1}) for kelts. No relationship existed between residence time in the inner estuary and either the temperature (Pearson's χ^2-test, p = 0.25) or salinity (Pearson's χ^2-test, p = 0.87) experienced on entry.
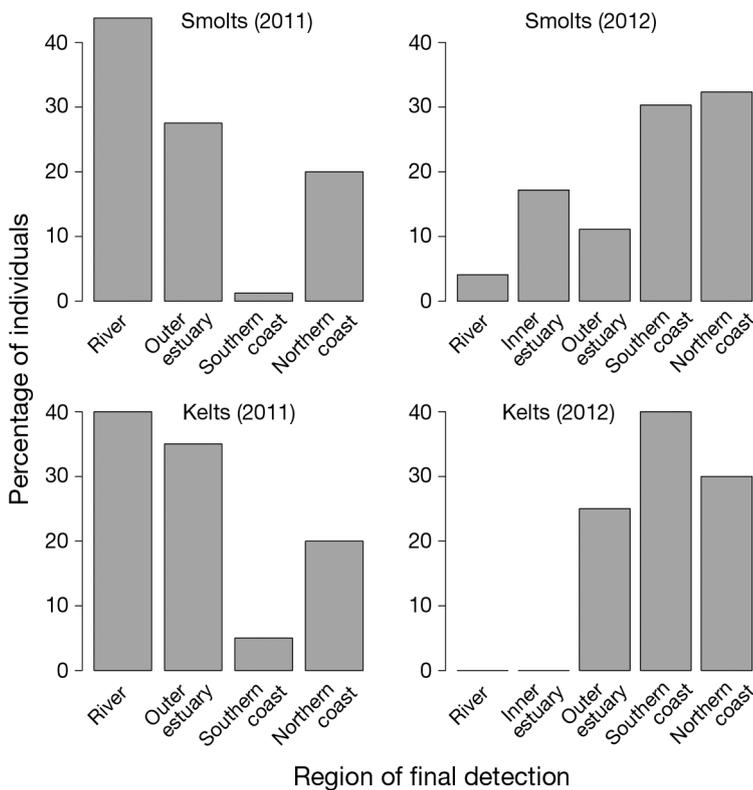

Fig. 5. Region of final detection of individual anadromous brown trout *Salmo trutta* for both 2011 and 2012 according to life stage: river, inner estuary (2012 only), outer estuary, southern coast, and northern coast

Table 4. Loss of anadromous brown trout *Salmo trutta* within the river and inner estuary

Year	Stage	No. released	No. detected in outer estuary	Loss (%)
2011	Smolts	80	39	51
	Kelts	20	12	40
2012	Smolts	99	73	26
	Kelts	20	19	5

Outer estuary and outer coast

Migration speed through the outer estuary did not change compared to the inner estuary for smolts (mean ± SD: 0.07 ± 0.07 BL s^{-1}; 0.12 ± 0.11 m s^{-1}; Kruskal-Wallis test: $\chi^2 = 1.39$, p = 0.24), but decreased for kelts (0.04 ± 0.04 BL s^{-1}; 0.17 ± 0.16 m s^{-1}: Kruskal-Wallis test: $\chi^2 = 2.91$, p = 0.01).

Individuals tended to use the north and the northwest passage when leaving the estuary (Fig. 4) (Pearson's χ^2-test, p < 0.001). After passing Receiver line 3 out towards the sea, there was little return to the estuary area (4 individuals [1 kelt, 3 smolts] in 2011 and 9 individuals [4 kelts, 5 smolts] in 2012). Migration within the Kattegat Sea was predominately in a northerly direction for both smolts and kelts in 2011, but no preference for north or south migration was observed in 2012 (Fig. 5). Overall ground speed along the north and south coast indicated a slower speed compared to the river and estuary, and kelts (0.032 ± 0.034 BL s^{-1} and 0.13 ± 0.15 m s^{-1}) showed a greater variation in ground speed than smolts (0.025 ± 0.22 BL s^{-1} and 0.05 ± 0.04 m s^{-1}); however, no direct comparison could be made due to the open nature of the outer coast.

Estimated mortality

Significantly higher loss of individuals was registered in the river and estuary in 2011 than in 2012, both for smolts (Pearson's χ^2-test, p < 0.001) and kelts (χ^2-test, p < 0.012). The total loss in the river and inner estuary was higher for smolts than for kelts in both years (Table 4), but this difference was not significant in 2011 (χ^2-test, p < 0.26) and only marginally significant in 2012 (χ^2-test, p < 0.037). The manual tracking revealed 5 individuals (1 kelt, 4 smolts)

Table 5. Instantaneous and daily mortality rates of anadromous brown trout *Salmo trutta* across the complete receiver array

Year	Stage	Instantaneous mortality rate (z)	Daily mortality rate (M) (% d^{-1})
2011	Smolts	2.1×10^{-2}	2.08
	Kelts	8.8×10^{-3}	0.87
2012	Smolts	9.3×10^{-3}	0.93
	Kelts	3.9×10^{-2}	0.39

in 2011 and 24 smolts in 2012 that did not leave the river; they were therefore classified as dead because all individuals were smoltified when tagged and should therefore have migrated. Instantaneous mortality rates from release until final detection across the entire array were greater for smolts than kelts and greater in 2011 than 2012 (Table 5).

DISCUSSION

In this study, we used acoustic telemetry to follow the sea trout migration of both smolts and kelts concurrently from a river, through a complex estuary and coastal system, and out into the sea. We found that the initial migration was nocturnal in the river and estuary but not along the coast. The groundspeed of both kelts and smolts decreased as the fish migrated farther out in the system. Within the river, life stage and discharge were found to affect migration speed, where kelts migrated faster than smolts in absolute terms, and migration speed increased with discharge. However, no difference was found between kelts and smolts in terms of groundspeed in the estuary and coast, contradicting previous studies on Atlantic salmon (Davidson et al. 2009, Haltunen et al. 2009). Mortality during the downstream migration was found to differ between years but not between kelts and smolts, also contradicting our hypothesis. We found evidence that brown trout followed the prevailing current in 2011, whereas no such pattern was observed in 2012.

River migration

River residency was shorter for kelts than smolts and decreased with increasing discharge (Table 2). Studies on kelts have indicated an increasing need for larger individuals to reach the sea to replenish their fat reserves after spawning, as larger individuals use a higher percentage of their energy stores during spawning (Jonsson & Jonsson 2003). The faster migration in males could not be explained by size and most likely lacks biological relevance, as the difference was less than 2 d. There is also a possibility that immature males were classified as females and therefore affected the results, but this is unlikely, as all tagged kelts had a very low condition factor and still showed signs of spawning coloration. A previous study on downstream river migration of kelts from the east coast of Sweden showed no effect of sex on migration speed or timing (Östergren & Rivinoja 2008). Kelts probably need to return to the sea faster in order to forage and to regain fat deposits lost during the spawning season and overwintering, and the overall low variation in kelt residency is likely an effect of their low condition after spawning and overwintering in the stream (Jonsson et al. 1997, Niemelä et al. 2000). An explanation for the variation in residence time of smolts in the river could be that the smolts began migration before they were fully smoltified and therefore needed to make stopovers in the river to fully smoltify before migrating out to sea, as has been observed in both brown trout and Atlantic salmon (McCormick et al. 1998, Moore et al. 1998). In agreement with earlier studies (Jonsson 1991, Jonsson & Jonsson 2002, Aldvén et al. 2015), migration was found to be stimulated by an increase in river discharge, supporting the idea that, in this system, smolts are awaiting the optimal environmental conditions. However, no effect of temperature on residence time within the river was found, suggesting that temperature only affects the initiation of migration and not migration speed per se (Aldvén et al. 2015). Individuals released later in the season migrated more quickly out of the system (Fig. 2), indicating an urge to leave, whereas individuals caught earlier during the season have the option to await the right conditions. Hence, the urgency for late migrators to leave the freshwater environment could reflect the limited time that the smolts are prepared (physiologically) to enter the sea (McCormick et al. 1987, Björnsson et al. 2011); if they remain too long in freshwater they could lose their ability for ion regulation (desmoltification). Proper timing is probably important for the smolts in order to lower their mortality and increase growth potential at sea (McCormick et al. 1997, Aldvén et al. 2015).

Inner estuary

Ground speeds for both kelts and smolts were lower across the inner estuary (between Riv2 and

Receiver line 1; Fig. 1) than in the river. The speeds in the estuary are similar to migration speeds observed in previous studies on brown trout smolts (Aarestrup et al. 2002, Thorstad et al. 2004, Finstad et al. 2005), and a lowered ground speed in the sea compared to the river has also been observed in a fjord system (Aarestrup et al. 2014). The lowered ground speed in the inner estuary could be caused by several factors. Firstly, the current velocity in the estuary was lower compared to the river, so there was less of a directional pressure in the same direction as the outward migration. Secondly, the separation between receivers in the river was in a gradient, with little room for sideways excursions, whereas migration in the estuary could occur in several directions alongside the net direction out towards the sea (Jepsen et al. 1998, Thorstad et al. 2004).

In smolts, exploration of the environment might be important for imprinting the cues of their home river in order to find their way back for spawning, and could be another plausible explanation for the reduced ground speed (Hansen & Jonsson 1994, Lucas et al. 2001). The kelts and smolts could also be spending time searching for a way to the outer estuary or feeding, yielding a lowered ground speed. However, other studies have shown a high mortality (23–90%) when fish need to pass through similar areas, making stopovers dangerous (Jepsen et al. 1998, Aarestrup et al. 1999, Olsson et al. 2001, Koed et al. 2006). As most predators in the system are visual hunters (e.g. Ardeidae and Pandionidae), the shallow estuary may pose an increased risk of predation during clearwater conditions (Gregory 1993, Gregory & Levings 1998). During periods of high water level with high turbidity, the potential predation risk would be lowered, which is also suggested from our data, where a higher estimated mortality was observed in 2011 (lower relative turbidity) than in 2012.

Outer estuary and coastal region

In the outer estuary and the coastal region, ground-speed decreased for both kelts and smolts, suggesting that migration was not in a unidirectional fashion, which may be an indication of increased foraging and exploration in the area. In support of this, previous studies on Atlantic salmon have indicated that kelts spend around 59% of their body lipid content during spawning (Jonsson et al. 1991, 1997), and are therefore in need of replenishing these reserves. When leaving the outer estuary, most individuals

traveled through the north and northwest passage in both years (Fig. 4). After leaving the outer estuary, brown trout moved in a northerly direction in 2011. The reason for this northward movement in 2011 could be that the brown trout were following the prevailing currents along the coast, which is in agreement with our hypothesis and has been observed in previous studies (Svärdson & Fagerström 1982, Degerman et al. 2012). However, in 2012, the migration routes were directed both north- and southwards, and the reason behind this discrepancy in migration routes remains unknown.

Mortality rates

Mortality varied between years in both kelts and smolts, with a greater mortality recorded in 2011. This greater mortality in the river/estuary in 2011 compared to 2012 is most likely explained by a difference in discharge, which was lower in 2011 compared to 2012, during the peaks of migration (Aldvén et al. 2015). The variation in mortality between years was also reflected in the number of individuals that were detected along the coast. A tendency for greater mortality in smolts compared to kelts was found, but only in 2012. This tendency is in line with our hypothesis that smolts should have a higher expected predation pressure compared to kelts (Jepsen et al. 1998, Aarestrup & Koed 2003, Skov et al. 2011). Another reason for this tendency could be that smolts make stopovers in the river and thereby become susceptible to predation in the lower reaches of the river or that they migrate to the sea before having fully smoltified (Virtanen et al. 1991, Staurnes et al. 1993, McCormick et al. 1998). The reason this pattern was not observed in 2011 could be a result of migration taking place during low discharge and clear water, making both smolts and kelts susceptible to bird (e.g. Ardeidae and Pandionidae) predation during the daytime, as some individuals remained for several days within the river and estuary. Migration peaks took place during peaks in discharge in turbid water. However, we infer that in order to avoid predation, a nocturnal migration pattern was adopted in all areas except the outer coast (Fig. 3). Several studies have observed similar nocturnal migration patterns in sea trout during the initial stage of migration and generally explain this as predator-avoidance behavior (Moore & Potter 1994, Moore et al. 1998, Aarestrup et al. 2014).

Manual tracking was performed during the study to evaluate the extent to which individuals died

within the river and inner estuary outside the bird sanctuary, as we were denied access to the bird sanctuary in 2011 and were only given access in 2012 for deployment and retrieval of the receivers. None of the fish that were lost in the estuary had been detected at any receiver at the end of the study, and they were therefore presumed dead. The combination of the manual tracking of individuals and the fact that no individuals lost in the inner estuary were detected again supports our estimates of mortality rates in this study. Similar mortality rates during outward migration have also been reported both for kelts (37 %, Aarestrup et al. 2015) and smolts (ranging from 26 to 76 %, Thorstad et al. 2007, del Villar-Guerra et al. 2014). Nevertheless, we cannot rule out the possibility that tag exclusion or differences in tag performance could have affected the observed difference in mortality. In addition, it is unlikely that the different tags would affect the fish differently, as they are very similar in size and shape. Any effect on the behavior or loss rates of the fish that the change in tag type might have had is likely to be very small if present at all and should not have affected our results in any manner. Range tests before each season revealed that the Thelma LP 7.3 tags had a slightly longer range (20–40 m) compared the Vemco V7 tags. However, no comparison between tags and tag performance was performed prior to the study, and to our knowledge, no extensive side-by-side study exists. We also cannot exclude the possibility that a passing fish was actually a predator (e.g. pike *Esox lucius* or kelts), as tags can remain inside a predator for several weeks after digestion (Armstrong et al. 1992).

CONCLUSION

In this study, we found a difference in mortality between years for both kelts and smolts (ranging between 5 and 51 %), but only a marginal difference between kelts and smolts. The underlying mechanism for this difference in mortality between years is likely caused by differences in discharge. Furthermore, the lack of difference in mortality between kelts and smolts in 2011 contradicts the theory that smolts should be more susceptible to predation compared to kelts. These results raise the question why some individuals remained within the estuary for an extended period, even though predation pressure was expected to be high. We also found diverging results with regard to migration routes. The theory that brown trout should follow the prevailing cur-

rents is consistent with the pattern observed in 2011 but not in 2012, and therefore needs further investigation. Migration speeds and diel migration patterns were consistent with previous studies indicating a general pattern of migration within different environments, most likely corresponding to foraging and predator avoidance. Our results are the first to report migration patterns and mortality rates from an open coastal system, knowledge that is necessary for effective stock management (e.g. closed areas and seasons, as well as size and harvest limitations). In order to implement successful management actions, it is important to further assess how different environmental factors (e.g. pollution) or effects from fish farms (such as sea lice) affect the observed mortality and migratory routes. Hence, future studies should focus on identifying the causes of the early marine mortality and to what extent it is possible to reduce it, but also the mechanisms that govern the decision to migrate in a certain direction once brown tout reach the open sea.

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